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Cytoarchitecture of the Medial Geniculate Body of Three Species of Bats: *Noctilio leporinus*, *Phyllostomus hastatus* and *Carollia perspicillata*

Andrew Adogwa[1], Venkatesan Sundaram[1*], I-sanna Gibbons[1] and Abayomi Odekunle[2]

[1]School of Veterinary Medicine, Faculty of Medical Sciences, The University of The West Indies, St. Augustine Trinidad, Trinidad and Tobago.
[2]School of Medicine, Faculty of Medical Sciences, The University of The West Indies, St. Augustine, Trinidad, Trinidad and Tobago.

Authors' contributions

This work was carried out in collaboration between all authors and all authors contributed equally. All authors read and approved the final manuscript.

Original Research Article

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ABSTRACT

The aim of the present study is to document cytoarchitectural details of Medial Geniculate Body (MGB) of the brain in three species of echolocating bats with different forage behavior. The brains were collected from six male adult bats of each species: *Noctilio leporinus* (fish-eating), *Phyllostomus hastatus* (carnivorous/ omnivorous) and *Carollia perspicillata* (fruit-eating) and were double-embedded and transverse serial sections were cut and stained with cresyl fast violet. The results showed that the mean length of the medial geniculate body was 1330 ± 115 µm in *N. leporinus*, 1210 ± 90 µm in *P.hastatus* and 790 ± 68 µm in *C. perspicillata*. The MGB of all three bats appeared to be divided into three divisions: dorsal (MGBd), ventral (MGBv) and medial (MGBm). These divisions were most distinct in the *N. leporinus* bat and least apparent in the *C. perspicillata*. In the *N. leporinus,* both dense-staining multipolar cells and light-staining round cells were located throughout the MGB. In the *P. hastatus*, the dense-staining multipolar cells were predominantly present in the ventral division of the middle third of the MGB, whereas light-staining round cells predominated at the rostral end of the MGB. Only light-staining round

**Corresponding author: Email: drvenkat1971@gmail.com;*

cells were seen throughout the MGB of the *C. perspicillata*. The large sized MGB and its clear subdivisions in *N. leporinus* suggests that it relies heavily on echolocation whereas *P.hastatus* and *C. perspicillata* use echolocation as well but also rely on hearing, smell and vision.

Keywords: Cytoarchitecture; medial geniculate body; bats.

1. INTRODUCTION

Most sensory information reaches the cortex via the thalamus through highly specific thalamocortical connections. In the auditory system, the medial geniculate body (MGB) provides thalamic input into the auditory cortex. The MGB is divided into three divisions, dorsal (MGBd), ventral (MGBv) and medial (MGBm) based on their neuronal morphology and density. The parallel thalamocortical pathways arise from the three distinct divisions of the MGB [1]. The MGBm is considered polysensory the MGBd, partly auditory and the MGBv entirely auditory [2]. Extensive work has been made on the MGB of both human and non-human primates [3] as well as on rats [4]. Among the echolocating animals, the auditory nuclei of dolphin and the bat has been studied in detail [5,6].

Many bats use echolocation for orientation in space and for detecting and capturing prey in total darkness [7,8,9,10,11]. The importance of hearing for survival has made these bats a focus for auditory research. Since, the different bats forage in different environment; it is assumed that different foraging strategies reflect on the development of the MGB, which is a thalamic relay nucleus between the inferior colliculus and auditory cortex in the auditory pathway. The information on the comparative cytoarchitecture of the auditory nuclei, specifically MGB of echolocating bats with different foraging strategies is lacking.

The neuroanatomical research on bats has been done mainly by using *Pteronotus parnelli* and *Rhinolophus rouxi* species [2,12,13]. The *Noctilio leporinus, Phyllostomus hastatus* and *Carollia perspicillata* are three species of bats used for the present study based on their differing foraging behavior. The *N. leporinus* bats eat small fish in both fresh and salt water but they need calm water surfaces in order to detect ripples. *P. hastatus* bats are omnivorous, feeding on flowers, pollen, insects and small vertebrates, forage on open and forested regions. *C. perspicillata* bats are mainly frugivorous. However, they may feed on insects and sometimes pollen which forage on moist evergreen and dry deciduous forests. These bats have been used in behavioral studies as well as physiological brain research and reproductive work. To the best of the authors knowledge no work has been reported on the MGB of these bats.

The present study is aimed to map out the location of the MGB in three species of bats and to compare the cytoarchitecture of the MGB of these bats and correlate the findings with their foraging behavior.

2. MATERIAL AND METHODS

For this present study six adult male live bats of each of the three species, *Noctilio leporinus, Phyllostomus hastatus* and *Carollia perspicillata* were collected. The average body weight of Noctilio leporinus, Phyllostomus hastatus and Carollia perspicillata were 60, 80 and 15 g respectively. Each bat was anaesthetized by using xylazine 2 mg/kg and ketamine 10 mg/kg

intramuscularly. The research protocol was approved by the institutional ethical committee. Immediately after euthanasia, the brains of the bats were removed, weighed and placed in 10% formal saline. The brains were manually processed and double embedded with celloidin and paraffin [14] as follows:

80% Alcohol	4 days
95% Alcohol	1 day
95% Alcohol	1 day
95% Alcohol	1 day
Absolute Alcohol/Ether	9 hours
Absolute Alcohol/Ether	9 hours
1% Celloidin	6 days
Chloroform	18 hours
Chloroform	18 hours
Paraffin 56°C - 58°C	12 hours
Paraffin 56°C - 58°C	12 hours

The tissues were then kept overnight at room temperature and then placed in paraffin for 2 hours in a vacuum under 20 inches of mercury pressure. The tissues were then blocked and sectioned at coronal plane at 10 µm using the rotary microtome MT 960. The sections were stained using cresyl fast violet. Digital images of the sections, size, shape and orientation of the cells were obtained with the aid of the Olympus BX51 system microscope and the Olympus DP71 microscope digital camera.

3. RESULTS

3.1 Medial Geniculate Body of *Noctilio leporinus* Bat

At the level of the superior colliculus, the most caudal end of the MGB appeared as a slight protrusion at the lateral aspect of the midbrain. The most rostral end of the pons was also seen at this level (Fig.1a). The caudal third of the MGB measured 1000 ± 85 µm in height and 800 ± 65 µm in width. The three divisions of into dorsal (MGBd), ventral (MGBv) and medial (MGBm) divisions were seen at this level. The MGBm comprised of dense-staining, multipolar cells measuring 10 to 12 µm in diameter (Fig.1d), while the rest of the MGB contained light-staining, round cells measuring 10 to 15 µm in diameter (Fig.1e). A few large spindle-shaped, foamy multipolar cells of 25 µm length were also seen mainly in the dorsal aspect of the MGBm (Fig.1f).

At the level of the commissure of the superior colliculus, the middle third of the MGB measured 1850 ± 165 µm in height and 2100 ± 180 µm in width. The MGBd and MGBm were more densely-populated than the MGBv (Fig.1b). The MGBd appeared to be further subdivided based on the cell density into a dense superficial and sparse deep part.

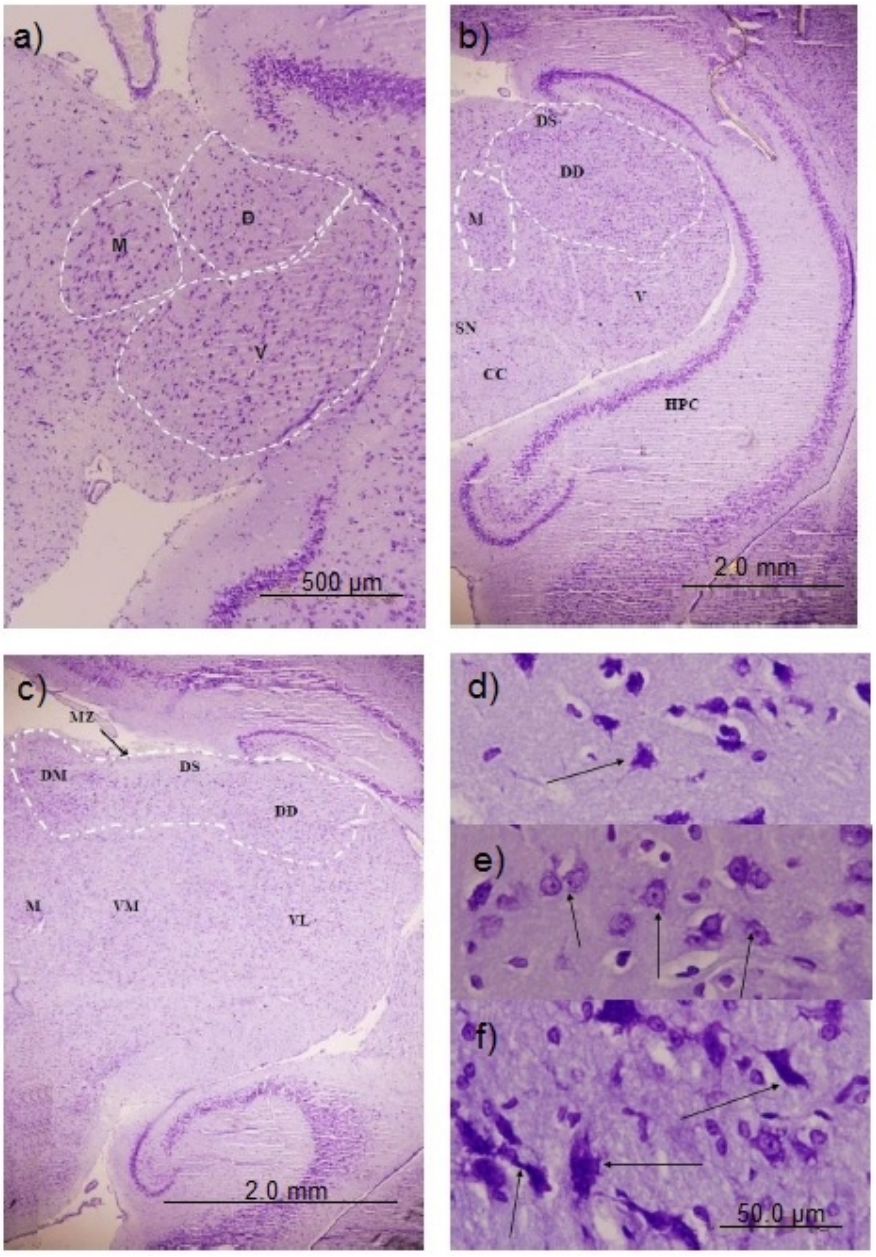
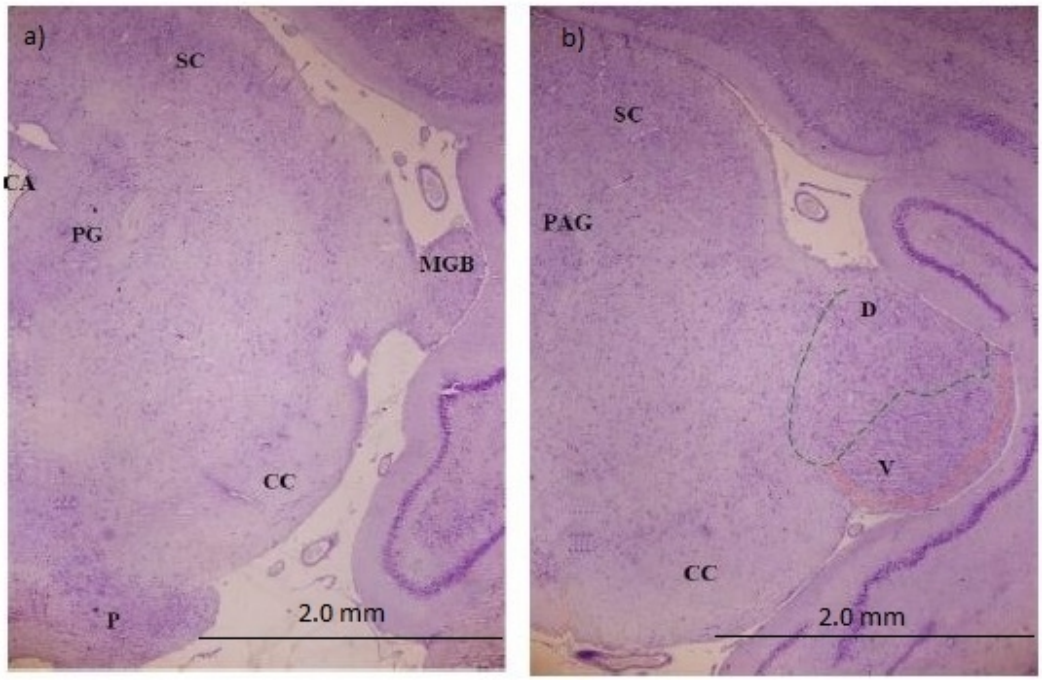


Fig. 1. Transverse section of the brainstem of *N.leporinus* showing (a) most caudal part (b) middle third and (c) rostral third of the MGB. (d) Dense staining multipolar cells (arrows) measuring 10 to 12 µm in diameter on the MGBm at the caudal MGB. (e) Light, round cells (arrows) measuring between 10 to 15 µm in diameter in the MGBv at the caudal MGB. (f) Spindle-like multipolar cells (arrows) measuring 25 µm in diameter in the MGBd of the caudal MGB. DS – Superficial part of the MGBd D- MGBd, DD – Deep part of the MGBd, V – MGBv, M – MGBm, HPC – Hippocampus, CC – Crus cerebri, SN – Substantia nigra, MZ – Marginal zone, DM – Medial portion of MGBd, VM – Medial portion of the MGBv, VL – Lateral portion of the MGBv.

The rostral third of the MGB was seen at the level of the fimbria of the hippocampus and measured 2065 ± 145 µm in height and 2300 ± 190 µm in width. The three divisions of the MGB were distinct at this level (Fig.1c). The MGBd composed of predominantly dense-staining multipolar cells measuring between 12.5 to 17.5 µm in diameter. A distinct collection of same type of cells was found medially along with the superficial layer and deep layer. The MGBv was the largest of the three divisions and appeared to be subdivided into two parts; lateral and medial. These parts were separated from each other by a cell-sparse area and both comprised dense-staining, elongated, multipolar cells, measuring between 17.5 to 22.5 µm in diameter. The MGBm comprised light-staining, round cells, measuring about 12.5 µm in diameter. Throughout the MGB, round, light-staining cells about 5 µm are seen. The MGB tapers off at the level of the internal capsule. The entire MGB of the *N. leporinus* bat measured 1330 ± 115 µm in length. The mean body and brain weight of this bat weighed as 48.1 ± 3.5 g and 6.93 ± 0.47 g respectively.

3.2 Medial Geniculate Body of *Phyllostomus hastatus* Bat

The MGB of this species first appeared caudally at the rostral level of the pons (Fig.2a). The caudal third of the MGB measured 900 ± 65 µm in height and 450 ± 55 µm in width. The MGBd and MGBv divisions alone could be distinguished at the caudal third of the MGB (Fig.2b). Light-staining, round cells were predominantly present throughout the MGB; however, a cluster of dense-staining multipolar cells was seen on the MGBv.



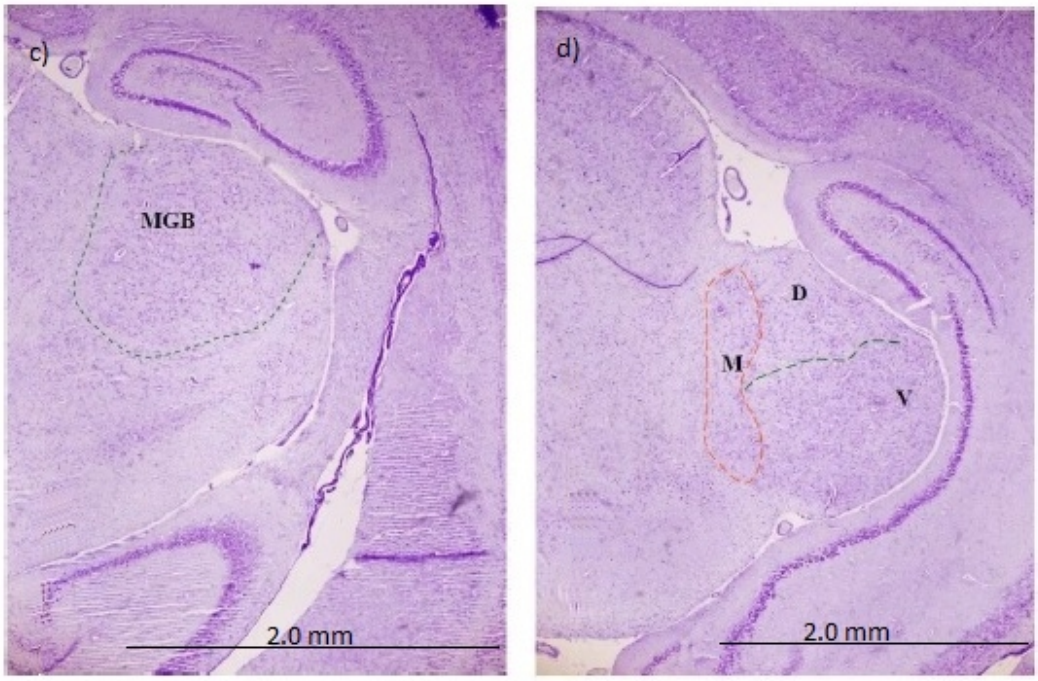


Fig. 2. Transverse section of the brainstem of the *P. hastatus* bat (a) most caudal part (b) caudal third (c) middle third and (d) rostral third of the MGB. CA-Cerebral aqueduct MGB-Medial geniculate body P-Pons SC – Superior colliculus PAG, PA – Periaqueductal grey CC – Crus cerebri D – MGBd V – MGBv M – MGBm

The middle third of the MGB measured 1300 ± 165 µm in height and 550 ± 35 µm in width. The three divisions were clearly distinguished at this level (Fig.2c). Large light-staining round cells of 15 µm diameter were seen mainly in the MGBd (Fig.3a).The MGBv appeared to be the largest of the three and contained mainly dense-staining elongated cells measuring about 13 µm in length and 5 µm in width with the long axis oriented dorsolaterally (Fig.3b). Few round cells were also seen in this division. Light-staining round cells were the predominant cells in the MGBm. This area was densely populated with the round cells (Fig.3c).

The rostral third of the MGB measured 1200 ± 76 µm in height and 600 ± 49 µm in width. It did not show any apparent divisions. Round, light-staining cells were the predominant cells seen (Fig.2d). The entire MGB of the *P. hastatus* bat measured 1210 ± 90 µm in length. The mean body and brain weight of this bat weighed as 73.24 ± 7.25 g and 8.57 ± 0.67 g respectively.

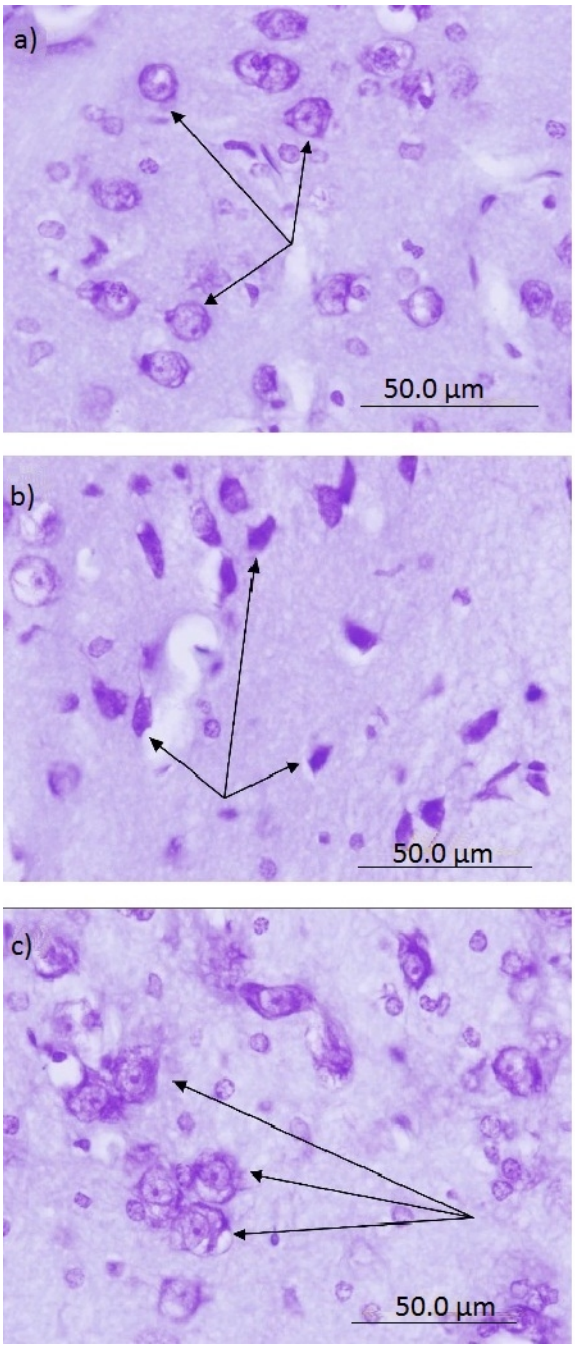
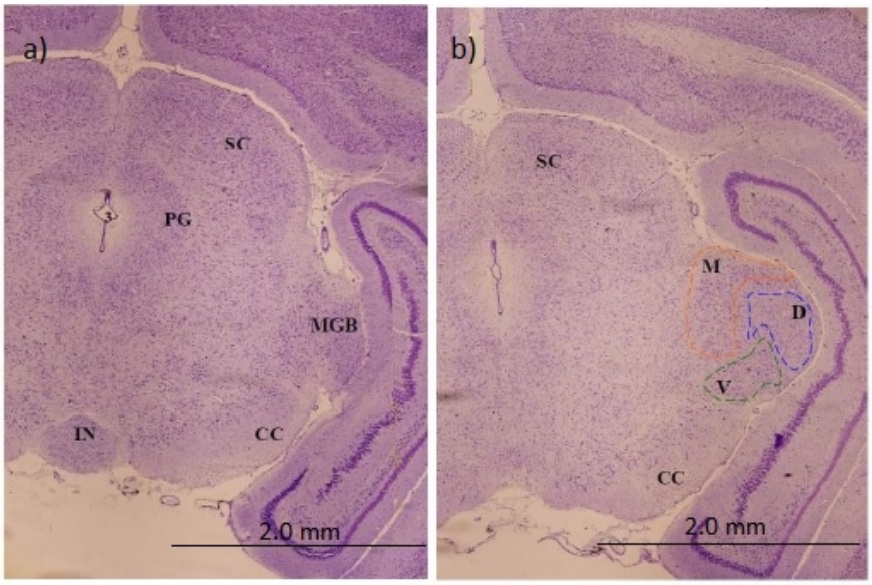


Fig. 3. Different types of cells in different regions of the MGB of the *P. hastatus* bat. (a) Large, light-staining round cells with a diameter of 15 µm (arrows) in the MGBd (b) Dark-staining elongated cells with a diameter of 13 µm (arrows) in MGBv (c) Dense, round light-staining cells with a diameter of 15 µm (arrows) in the MGBm.

3.3 Medial Geniculate Body of *Carollia perspicillata* Bat

At the level of the interpeduncular nucleus and the rostral pole of the pons, the caudal third of the MGB was visible and measured 940 ± 78 µm in height and 400 ± 35 µm in width (Fig.4a). The all three divisions of the MGB were visible (Fig.4b) and multipolar cells made up the majority of the MGB at this level. Some of the multipolar cells were large (20.0 µm in diameter) while others were medium (12.5 µm in diameter) in size (Fig.4d and 4e). However, a few small (5.0 µm in diameter) round cells were also present. The MGBm appeared more cell-dense than the rest of the MGB. The MGBv was densely populated and contained predominantly multipolar, dense-staining cells (Fig.4f); while the MGBd appeared less cell-dense and comprised light-staining, round cells (Fig.4g and 4h). Dense-staining multipolar cells were seen in the rest of the MGB with the MGBv appearing denser than the MGBd.



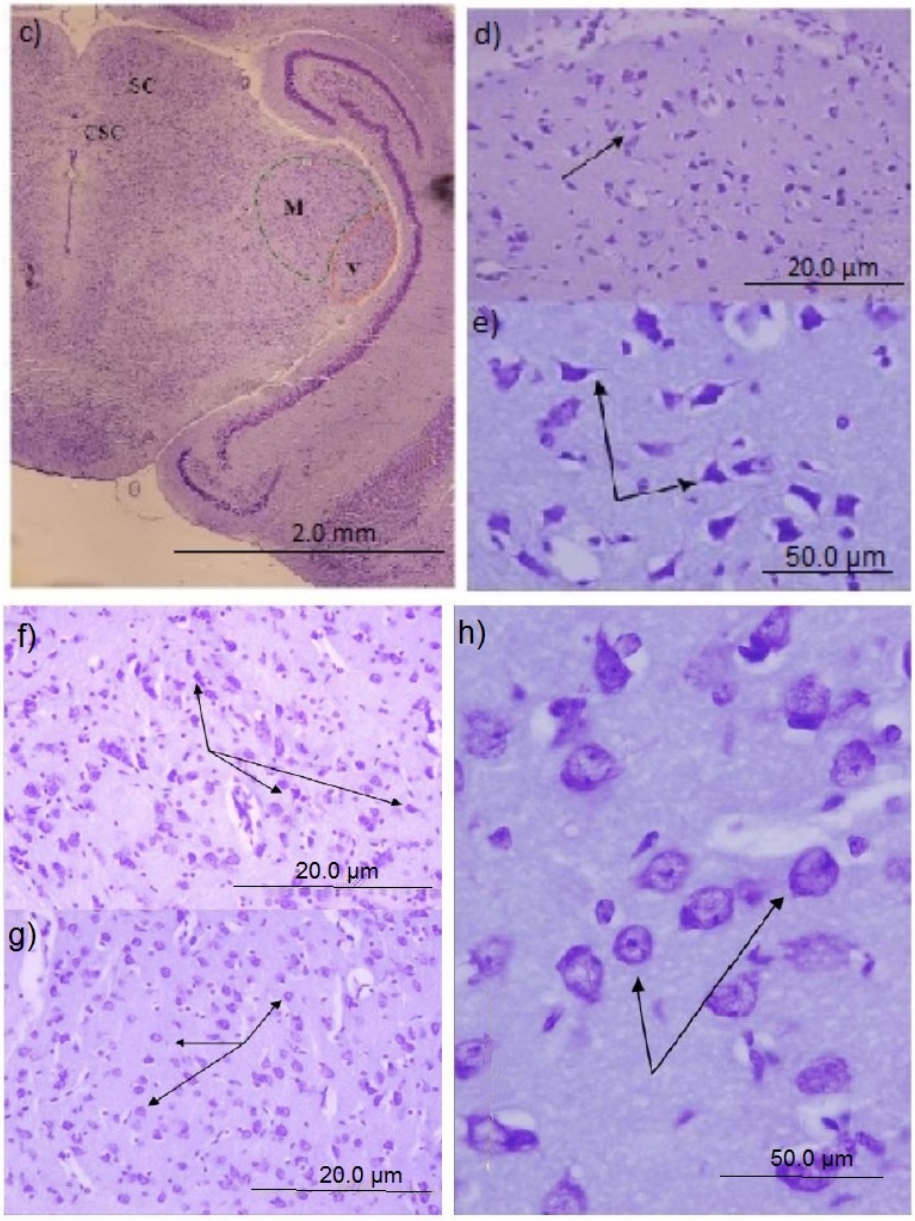


Fig. 4. Transverse section of the brainstem at the level of the *C. perspicillata* bat showing (a) caudal third of the MGB and (b) its subdivisions (c) middle third of the MGB and its subdivisions. (d), (e) Multipolar cells (arrows) in the MGB. (f) Multipolar cells (arrows) predominate in MGBv. (g,h) Round cells (arrows) predominate in MGBd. MGB-Medial geniculate body CA-Cerebral aqueduct PG-Periaqueductal grey IN-Interpeduncular nucleus SC – Superior colliculus CC – Crus cerebri M – Medial division of the MGB D – Dorsal division of the MGB V – ventral division of the MGB CSC – Commissure of the superior colliculi

At the level of the commissure of the rostral colliculus, the middle third of the MGB measured 1200 ± 93 µm in height and 950 ± 62 µm in width and only two divisions were apparent (Fig.4c). The MGBm now comprised mainly round lightly-stained cells measuring between 12.5 µm and 15.0 µm in diameter (Fig.4h) and also a few multipolar lightly-stained cells. The rest of the MGB contained the same types of cells but MGBv was less dense and the cells were uniformly distributed.

The rostral third of the MGB measured 1250 ± 86 µm in height and 1300 ± 97 µm in width. At this level, lightly-stained round cells were uniformly distributed throughout the entire MGB and no obvious subdivisions were present. The entire MGB of the *C. perspicillata* bat measured 790 ± 68 µm rostrocaudally. The mean body and brain weight of this bat weighed as 14.4 ± 2.1 g and 3.74 ± 0.75 g respectively.

4. DISCUSSION

The MGB was abutted from the tegmentum of the midbrain and extended into the diencephalon in all the bats studied as in humans [3]. It measured 1330 ± 115 µm in the *N. leporinus*, 1210 ± 90 µm in the *P. hastatus* and 790 ± 68 µm in the *C. perspicillata* bat. The auditory nuclei are relatively larger in echolocating animals like the marmoset [15], dolphins [16,17] and bats [6] than the human and non-human primates [10] which is similar in the present study as the N.leporinus is heavily depend on the echolocation than the other bats [10].

The insectivores bats rely heavily on echolocation for the pursuit of and capture of prey would have larger auditory nuclei than do phytophagus species. The *Phyllostomus* species which also echolocate while foraging but the size of the auditory nuclei is smaller when compare with the *N.leporinus* [18]. The size and brain weight do not reflect proportionately on the size of the MGB in the present study as the body and brain weight of the *P. hastatus* measured as 73.24 ± 7.25 g and 8.57 ± 0.67 g respectively which is higher than the *N.leporinus* 48.1 ± 3.5 g and 6.93 ± 0.47 g, whereas the length of the MGB measured 1210 ± 90 µm in *P.hastatus* and 1330 ± 115 µm in *N.leporinus.*

The three divisions of the MGB viz. MGBd, MGBv and the MGBm based on cellular architecture and disposition were noticed in all the bats studied which is similar to those reported in the human [1], and the rabbit [19], whereas MGB represented only two divisions; MGBd and MGBv in the sheep, pig [19], dolphin [20], cats [21] and monkeys [22]. The medial division is considered polysensory [23]; the dorsal, partly auditory [2,23] and the ventral entirely auditory [23,24]. However, the divisions were most obvious in the *N.leporinus* bats and least in the *C.perspicillata* bats. In the present study, further subdivisions of the MGB were also noted. The middle third of the MGB of the *N. leporinus* bat revealed a subdivision of the MGBd into superficial and deep parts. In this bat, MGBv also comprised of two parts: lateral and medial in the rostral third of the MGB. These results were anticipated since it is known that the *N. leporinus* bat uses echolocation as a major part of its feeding strategy [25, 26]. Similar subdivisions were also seen in the rat [4]: superficial and deep parts of the MGBd and both the ventral nucleus and the pars ovoidea of the MGBv were seen.

In the sheep, pig and cat [21,27], the MGBd comprises loosely packed cells whereas MGBv is densely packed and subdivided into a smaller medial part with large cells and a larger lateral part with small cells. In the rabbit [19], the MGBd and MGBm are composed of loosely arranged large cells and the MGBv of densely-packed small cells. In humans(1), the MGBd

contains mainly small and medium-sized cells, the MGBv mainly large cells with some small cells and the MGBm contains very large cells (the largest cells in all the divisions of MGB) with numerous small cells. In the present study, the loosely packed round cells were found mainly in the rostral third of the MGBv in the *N.leporinus* bat and in the middle and rostral third in the *P. hastatus* and *C. perspicillata* bats.

The cell composition of the MGB in this study is similar to those of the dolphins [20], cat [21] and the monkey [22]. The parvocellular (anteromedial part with small-cells) part and the magnocellular (medioventral part with large cells) part are similar to the MGBd and MGBv divisions of the present study. The MGB in this study as in the dolphin and the cat contains densely packed small round cells evenly distributed throughout the nucleus. The MGB of the galago and the slow loris[28] comprises of mainly the parvocellular part made up of small to medium-sized cells. Few large cells scattered in the caudoventral part of the nucleus represent the magnocellular part.

The MGB comprises of a parvocellular (anteromedial) and a magnocellular (medioventral) in the dolphins [20], cats [21] and monkeys [22] which is comparable to the MGBd and MGBv in the present study. The parvocellular division is the main acoustic nucleus of the thalamus projects exclusively to the auditory cortex [5]. The MGB of the dolphins and cats contain densely packed small round cells that are uniformly distributed which are similar to the findings in the present study; however, the magnocellular division was described as a small area comprising large, scattered, pale cells. The parvocellular division is bordered by the nucleus suprageniculatus, comprises of large scattered cells in dolphins [5]. Similarly, the suprageniculate nucleus of the cat contains stellate cells with large perikarya [29]. However, the portion identified as the suprageniculate nucleus in the present study was the superficial part of the MGBd which is cell-dense area unlike the dolphins where they are scattered cells and this division is found only in the *N. leporinus* bats.

The MGB of the galago and the slow loris comprises mainly the parvocellular part with moderately stained small to medium sized cells [30]. Large, dark-staining cells were seen at the level of the nucleus limitans and it was surmised that these were of the magnocellular division. Few large cells scattered in the caudoventral portion of the nucleus in the galago and the slow loris. In the present study, large round cells were found mainly in the MGBm and distributed uniformly throughout MGB at its rostral third. These cells, however, were not darkly stained.

The findings of this study revealed that although the MGB is large in bats generally, there appears to be differences among the species. The large size of the MGB of the *N. leporinus* bat and its distinct subdivisions compared to the other two species are probably due to the fact that it relies heavily on echolocation in order to feed [26]. The *P. hastatus* and the *C. perspicillata* use echolocation as well but also rely on hearing, vision and smell [8,30,31,32,33]

5. CONCLUSION

Both multipolar and round cells were found in the medial geniculate body (MGB) of the *N. leporinus* and *P. hastatus*; whereas mainly round cells were seen in the MGB of the *C. perspicillata.* Three main subdivisions of the MGB were seen: MGBd, MGBv and MGBm. These divisions were clearly seen in the *N. leporinus* and were the least distinguished in the *C. perspicillata*. It was also noted that in the *N. leporinus*, the MGBd was further divided into deep and superficial parts and MGBv into medial and lateral parts. The large sized MGB and

its clear subdivisions in *N. leporinus* suggests that it relies heavily on echolocation whereas *P. hastatus* and *C. perspicillata* use echolocation as well but also rely on hearing, vision and smell.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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